AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 111:519–530 (2000)

Rib Remodeling Dynamics in a Skeletal Population From Kulubnarti, Nubia

DAWN M. MULHERN*
Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0112

KEY WORDS osteon; bone formation rate; activation frequency; effective age of adult compacta; Nubia

ABSTRACT Bone remodeling variables in the rib were analyzed for a skeletal population of medieval antiquity (ca. A.D. 550–1450) from Kulubnarti, in Sudanese Nubia. The skeletal remains are naturally mummified and in an excellent state of preservation. The study sample consists of thin sections from the ribs of 80 individuals, ranging in age from 15–50+ years.

Ribs were examined using a standard microscope and image analysis software. Numbers of intact osteons, fragmentary osteons, forming osteons, and resorption spaces were counted, osteon and Haversian canal areas were measured, and several variables were calculated to assess morphometric and remodeling status in the rib. Variables calculated included mean annual activation frequency, mean bone formation rate, and net osteonal remodeling.

Results indicate that age changes are consistent with those observed for other archaeological and modern samples. High numbers of resorption spaces in young males may reflect slower skeletal development in boys compared to girls. Comparisons of rib data with results of a previous study on patterns of femoral bone remodeling in the same population indicate that ribs have more osteons and higher bone formation rates compared to the femur. Also, sexual differences in osteon size observed in the femur were not observed in the rib. Activation frequency and bone formation rate are low in the Kulubnarti population compared to previously published data for a modern sample, a finding consistent with reported results from other archaeological samples. Genetic factors influencing the minimum effective strain setpoint and duration of skeletal maturation, in addition to repetitive high strains at Kulubnarti, may contribute to observed differences. Am J Phys Anthropol 111: 519–530, 2000.

During life, bone is a dynamic tissue that responds to the physiological, nutritional, and mechanical demands of the human body. A number of researchers studying bone growth and maintenance have focused on the relationship between bone histology and various stressful factors in order to learn more about the lifeways of ancient communities. For example, Burr et al. (1990) identified differences between the sexes in osteon number and dimensions in the femur that may have indicated differential response to intense physical activity in a Pecos Indian sample. Studies of the femur by Martin and Armelagos (1979) and Martin (1983) on a Nubian population from Wadi Halfa and by Prendergast-Moore (1987) on a Nubian population from Kulubnarti suggest that the bone loss seen in

Grant sponsor: Graduate School, University of Colorado at Boulder.

*Correspondence to: Dawn M. Mulhern, 5830 High Bluff Court, Burke, VA 22015. E-mail: Mulhern.Dawn@nmnh.si.edu

Received 17 March 1999; accepted 30 November 1999.

young Nubian females is associated with pregnancy and lactation. Stout (1976, 1978) attributed high rib osteon density from the Ledders site in the Lower Illinois River Valley to secondary hyperparathyroidism resulting from a maize diet.

Human skeletal remains from the medieval site of Kulubnarti, Nubia have been studied extensively for the purpose of reconstructing the biocultural adaptations of this ancient community. The excellent preservation of these mummified remains has provided the opportunity for macroscopic, microscopic, chemical, and genetic analyses to be conducted since their disinterment in 1979. Previous studies of fracture rates (Burrell et al., 1986; Kilgore et al., 1997) and degenerative disease (Kilgore, 1984) have demonstrated a clear pattern of mechanical stress.

Studies of bone growth, development, and aging have also been an integral part of the ongoing research directed toward gaining an understanding of life at Kulubnarti. A recent study by Mulhern and Van Gerven (1997) identified differences between the sexes in femur histomorphometry that may reflect differential responses to physical strain at Kulubnarti. A mechanical explanation for the observed differences would be supported if the rib (a nonweight-bearing bone) does not exhibit morphometric differences between the sexes. The present research further investigates this relationship through a comparison of compact bone organization in the femur and rib.

The purpose of this research is to present new data for patterns of bone organization and maintenance in the rib for a skeletal population from Kulubnarti, Nubia, dating to Nubia's medieval period (ca. A.D. 550–1450). Additionally, these data are used for comparisons between the rib and the femur. If the sexual differences observed in the femur are not observed in the rib, an argument for differences due to mechanical demands is strengthened. Finally, rib remodeling at Kulubnarti is compared to rib remodeling in other archaeological populations, so that differences can be studied in the context of environment.

MATERIALS

The skeletal sample chosen for this study is from the mainland cemetery (21-R-2) at Kulubnarti, that may span Nubia's entire medieval period (ca. A.D. 550–1450). This sample includes remains from 218 mummified or partially mummified individuals, in an excellent state of preservation.

Kulubnarti is an island situated in a desolate region of Upper Nubia between the Second and Dal Cataracts of the Nile in modern-day Sudan, known as the *Batn el Hajar*, or "belly of rock." Adams (1977) described this harsh, rugged landscape as "the most barren and forbidding of all Nubian environments." This area of Nubia was sparsely populated by farming communities, such as the one that lived at Kulubnarti. Agriculture was made possible only through use of technological developments, such as the use of a *saquia*, or water wheel, and retaining walls that protected alluvial soils from floods. The staple crops included sorghum, millet, barley, beans, lentils, peas, dates, and wheat. Cattle, sheep, and pigs provided Kulubnarti Nubians with limited protein (Adams, 1977; Van Gerven et al., 1990).

Largely through Egyptian influence, Nubia was converted to Christianity by A.D. 550. One century later, Egypt fell to Islamic armies, but a Christian king continued to rule Nubia. This allowance was made as the result of the *Baqt*, a treaty that ensured Nubia's autonomy at the price of paying annual tribute to the Imam. From the ninth to the twelfth century, Nubia enjoyed a prosperous economic and cultural period. The political climate during Nubia's late medieval period became tumultuous, as its Christian kingdom experienced increasing pressure by Moslem forces. A Moslem prince took power in Dongola during the twelfth century, and the *Batn el Hajar* became a refuge area to which Christians fled from both the North and South. With this change, Nubia made the transition from a prosperous medieval period to a feudal "dark" age that continued until the sixteenth century (Adams, 1977; Van Gerven et al., 1990).

TABLE 1. Sample distribution by age, sex, and bone

Age (years)	Rib		Femur	
	Females	Males	Females	Males
15–19	7	3	0	0
20–29	8	7	6	6
30–39	12	10	6	6
40–49	11	14	6	6
50+	7	1	6	1
Total	45	35	24	19

The study sample for the present research consists of rib thin sections from 80 adolescent and adult individuals, ranging from 15–50+ years at age of death. Two sections were taken from the middle third of the sixth rib for each individual. In addition, midshaft femoral samples from 43 adults ranging from 20–50+ years are used for comparison. Detailed methods and results of the femoral analysis are reported elsewhere (Mulhern, 1994; Mulhern and Van Gerven, 1997). Thirty-four individuals are represented in both the femur and the rib samples. The sample distribution by age, sex, and bone is given in Table 1. Sex determination was made based on pelvic morphology and soft tissue, including the presence of genitalia and facial hair when possible. Remains were seriated by age at death using multiple indicators, including the morphology of the os pubis, degenerative joint changes, and dental attrition (Van Gerven et al., 1981).

METHODS

Samples were taken from the middle third of the sixth rib. The Kulubnarti remains are so well preserved that virtually all of the ribs are present, making positive identification of rib number possible in most cases. Two thin sections were prepared for each of 80 ribs, for a total of 160 sections.

Sample preparation was conducted by Jim Harrington at the Thin Section Laboratory in Bellingham, Washington. Each specimen was sawed into $\frac{1}{4}$ to $\frac{1}{2}$ inch slabs. If friable, it was first coated with epoxy and allowed to dry. The specimen was then impregnated with Epoxylite 301 and isopropyl alcohol under a strong vacuum with alternating atmospheric pressure. Small sections (less than $\frac{3}{4}$ inch in diameter) were dried in an oven. All specimens were ground using 600 grit and then dried on a hot plate for 1–4 hr. Each section was mounted using Epoxylite 301. After hardening, excess epoxy was removed by sawing or grinding, using an oil bath saw or oil grinder. Each section was then ground with 320 grit in alcohol or Pella A oil to about 70 μm. Grinding was finished in a 600 grit alcohol or oil slurry to about 40 μm.

Following preparation, histomorphometric analysis of the ribs was conducted using a standard compound light microscope, Cue-2 Olympus Image Analyzer Software (described by Galai, 1991) and the public domain NIH image program (developed at the U.S. National Institutes of Health).

The following 13 variables were analyzed and values were averaged for two rib sections per individual; the nine variables that were previously analyzed for the femur (Mulhern and Van Gerven, 1997) are indicated by an asterisk. Analysis is consistent with methods outlined by Frost and Wu (1967), Wu et al. (1970), Stout and Teitelbaum (1976), Frost (1987b), and Stout and Paine (1994).

1. *Intact osteon density (IO): number of complete osteons per unit area (a complete osteon is one in which at least 90% of the Haversian canal is unremodeled), counted for each entire rib section.
2. *Fragmentary osteon density (FR): number of fragmentary osteons per unit area (a fragmentary osteon is one in which 10% or more of the Haversian canal has been remodeled), counted for each entire rib section.
3. Forming osteon density (FO): number of forming osteons per unit area. Forming osteons were identified as those with at least some evidence of refilling (concentric lamellae), but with large Haversian canals (at least 50% larger than complete canals). It is probable that the number of forming osteons is undercounted, since osteons that were close to completion were not identified.
4. Resorption space density (RS): number of resorption spaces per unit area.
5. *Haversian canal area (HcA): average area of Haversian canals, based on mea-

surements of 25 canals per individual for the rib (80 canals for the femur).

6. *Osteon area (OA): average area of osteons (including their Haversian canals), based on measurements of 25 osteons per individual for the rib (80 for the femur). Twenty-five osteons were measured for the rib, for consistency with Stout and Paine (1994). An attempt was made to measure osteons with a complete outer reversal line from the periosteal, middle, and endosteal envelopes.
7. *Mean osteonal cross sectional area (A_h): average area of bone per complete secondary osteon (bone between the cement line and Haversian canal), based on 25 osteons per rib (80 per femur). This variable was calculated using the following formula:

$$A_h = \mathrm{OA} - HcA$$

8. *Mean cross-sectional diameter (D_h): diameter of complete osteons, calculated using the mean osteonal cross sectional area using the following formula:

$$D_h = (4A_h/\pi)^{-2}$$

9. *Osteon population density (OPD): total number of intact and fragmentary osteons, calculated using the following formula:

$$\mathrm{OPD} = \mathrm{IO} + \mathrm{FR}$$

10. *Accumulated osteon creations (AOC): total number of intact, fragmentary and missing osteons for a given OPD; calculated using the following formula:

$$\mathrm{AOC} = \mathrm{IO} + \mathrm{FR} + \text{Missing Osteons}$$

Osteon population density increases with age until an asymptote is reached, when each new osteon creation removes evidence of an earlier osteon creation. Frost (1987b) provided a method for estimating missing osteons that was applied to an archaeological sample by Stout and Paine (1994). The algorithm used to account for missing osteons uses a scaling operator, β, which can be multiplied by OPD to estimate AOC. β is the AOC/OPD ratio and is calculated using the following formula:

$$\beta = (1 - a^x)^{-1}$$

where a = OPD is normalized to its predicted asymptote, or:

$$a = \mathrm{OPD}(\mathrm{OPD\ asymptote})^{-1}$$

and x = 3.5, according to the analysis by Frost (1987b) of previously published data. The OPD asymptote can be estimated for each specimen using the following formula:

$$\mathrm{OPD\ asymptote} = k[D_h)^2]^{-1}$$

where k = a fragmentary osteon packing factor that accounts for a higher number of intact plus fragmentary osteons than can be predicted based on a theoretical limit of intact osteons alone; k is calculated using the following formula:

$$k = (\mathrm{OPD\ asymptote})(D_h)^2$$

The packing factor k should be based on an independent sample of individuals aged 50+ at age of death. Stout and Paine (1994) reported a k value of 1.7 for a sample of cadavers of known age. The OPD asymptote that they observed for this sample was 36.2/mm^2. Mean osteonal cross-sectional area was determined to be 0.047 mm, based on measurements of a large clinical sample by Wu et al. (1970). This k value was used for the packing factor for the rib. As reported in Mulhern and Van Gerven (1997), a value of k = 1.38 was used for the femur. This value was reported by Abbott et al. (1996) to be more appropriate for the femur because the asymptote is closer to 30/mm^2. AOC was then calculated for each individual using the following formula:

$$\mathrm{AOC} = (\beta)(\mathrm{OPD})$$

11. Mean activation frequency (μ_{RC}): mean number of osteons created annually per mm^2, calculated using the following formula:

TABLE 2. Descriptive statistics by age and sex[1]

Sex	Age (years)	IO (n/mm^2)	FR (n/mm^2)	FO (n/mm^2)	RS (n/mm^2)	HcA (mm^2)	OA (mm^2)
F	15–19	4.72 ± 0.35	0.91 ± 0.14	0.66 ± 0.05	0.94 ± 0.12	0.0012 ± 0.00001	0.035 ± 0.0049
	20–29	10.04 ± 0.61	2.41 ± 0.22	0.79 ± 0.07	0.39 ± 0.05	0.0010 ± 0.00007	0.033 ± 0.0007
	30–39	12.87 ± 0.29	3.46 ± 0.14	0.72 ± 0.03	0.49 ± 0.02	0.0011 ± 0.00003	0.038 ± 0.0009
	40–49	13.14 ± 0.16	4.13 ± 0.27	1.20 ± 0.08	0.61 ± 0.03	0.0011 ± 0.00003	0.037 ± 0.0006
	50+	12.92 ± 0.56	5.41 ± 0.33	2.26 ± 0.32	0.82 ± 0.05	0.0011 ± 0.00004	0.032 ± 0.0008
M	15–19	5.71 ± 0.39	1.45 ± 0.21	0.79 ± 0.19	2.31 ± 0.22	0.0013 ± 0.00001	0.039 ± 0.0017
	20–29	9.04 ± 0.30	2.91 ± 0.28	0.80 ± 0.06	0.50 ± 0.12	0.0012 ± 0.00004	0.043 ± 0.0019
	30–39	11.55 ± 0.38	3.13 ± 0.16	0.71 ± 0.03	0.49 ± 0.05	0.0011 ± 0.00003	0.036 ± 0.0013
	40–49	11.94 ± 0.26	4.10 ± 0.21	1.26 ± 0.04	0.64 ± 0.04	0.0010 ± 0.00003	0.033 ± 0.0008
	50+	10.81 ± N/A	4.71 ± N/A	4.58 ± N/A	1.27 ± N/A	0.0011 ± N/A	0.032 ± N/A

[1] Values are mean ± SD. F, female; M, male; IO, intact osteon number; FR, fragmentary osteon number; FO, forming osteon number; RS, resorption space number; HcA, Haversian canal area; OA, osteon area.

TABLE 3. Descriptive statistics by age and sex[1]

Sex	Age (years)	A_h (mm^2)	D_h (mm^2)	OPD (n/mm^2)	AOC (n/mm^2)	μ_{RC} (n/mm^2/year)	$V_{f,r,t}$ (mm^2/mm^2/year)	net $V_{f,r,t}$ (mm^2/mm^2)
F	15–19	0.034 ± 0.0008	0.203 ± 0.002	5.63 ± 0.20	5.67 ± 0.20	1.72 ± 0.08	0.062 ± 0.009	0.204 ± 0.009
	20–29	0.032 ± 0.0007	0.201 ± 0.003	12.45 ± 0.82	13.78 ± 1.05	1.08 ± 0.07	0.037 ± 0.003	0.480 ± 0.045
	30–39	0.037 ± 0.0009	0.214 ± 0.003	16.33 ± 0.41	19.09 ± 0.64	0.86 ± 0.03	0.033 ± 0.002	0.723 ± 0.034
	40–49	0.036 ± 0.0006	0.213 ± 0.002	17.28 ± 0.30	20.03 ± 0.51	0.67 ± 0.02	0.025 ± 0.0007	0.742 ± 0.023
	50+	0.031 ± 0.0008	0.199 ± 0.003	18.33 ± 0.54	19.93 ± 0.73	0.52 ± 0.02	0.016 ± 0.0008	0.634 ± 0.031
M	15–19	0.038 ± 0.002	0.220 ± 0.005	7.15 ± 0.86	7.19 ± 0.05	1.96 ± 0.25	0.073 ± 0.007	0.276 ± 0.023
	20–29	0.042 ± 0.002	0.228 ± 0.006	11.94 ± 0.57	13.49 ± 0.81	1.35 ± 0.10	0.062 ± 0.006	0.613 ± 0.055
	30–39	0.035 ± 0.001	0.208 ± 0.004	14.67 ± 0.53	15.82 ± 0.67	0.68 ± 0.03	0.023 ± 0.001	0.553 ± 0.026
	40–49	0.032 ± 0.0008	0.200 ± 0.002	15.61 ± 0.35	18.92 ± 0.78	0.61 ± 0.03	0.021 ± 0.001	0.665 ± 0.042
	50+	0.031 ± N/A	0.197 ± N/A	15.53 ± N/A	15.94 ± N/A	0.40 ± N/A	0.012 ± N/A	0.487 ± N/A

[1] Values are mean ± SD. F, female; M, male; A_h, mean osteonal cross-sectional area; D_h, mean osteonal cross-sectional diameter; OPD, osteon population density; AOC, accumulated osteon creations; μ_{RC}, mean annual activation rate; $V_{f,r,t}$, mean annual bone formation rate; net $V_{f,r,t}$, net osteonal remodeling.

AOC/(chronological age

$-$ 12.5 years)

where 12.5 years is the age of the effective birth of adult compacta in the middle third of the sixth rib, when half of the original bone has been replaced by adult bone, and (chronological age $-$ 12.5 years) represents the effective mean age of the adult compacta (Frost and Wu, 1967).

12. Bone remodeling rate ($V_{f,r,t}$): estimated bone formation rate of an individual, based on the effective mean age of their adult compacta, calculated using the following formula:

$$V_{f,r,t} = (\mu_{RC_h})$$

13. *Net osteonal remodeling (net $V_{f,r,t}$): total amount of remodeling that occurred over an individual's lifetime, calculated using the following formula:

$$\text{net } V_{f,r,t} = (AOC)(A_h)$$

Data analysis was conducted using SPSS software, version 4.0 (Language Systems Corp., Chicago, IL). The variables assessed were compared between sexes, between bones, and among age categories using multiway analysis of variance tests (MANOVA).

RESULTS

Age differences

Detailed results for the analysis of the femur can be found in Mulhern and Van Gerven (1997). Results for the rib are presented here. Tables 2 and 3 summarize the results of the histomorphometric analysis by age and sex. There is only one male representing the 50+ age category, but counts and measurements are presented for comparisons.

Both sexes exhibited statistically significant age-related differences in most variables, including IO ($P < 0.0001$), FR ($P < 0.01$), FO ($P < 0.0001$), RS ($P < 0.01$), OPD ($P < 0.0001$), AOC ($P < 0.001$), μ_{RC} ($P <$

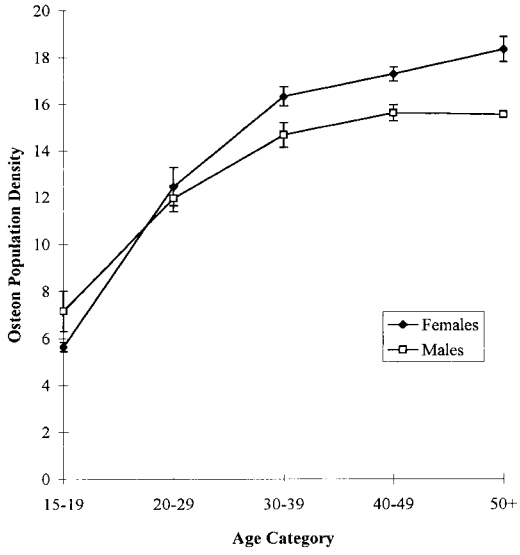

Figure 1. Osteon population density (n/mm^2) by age and sex.

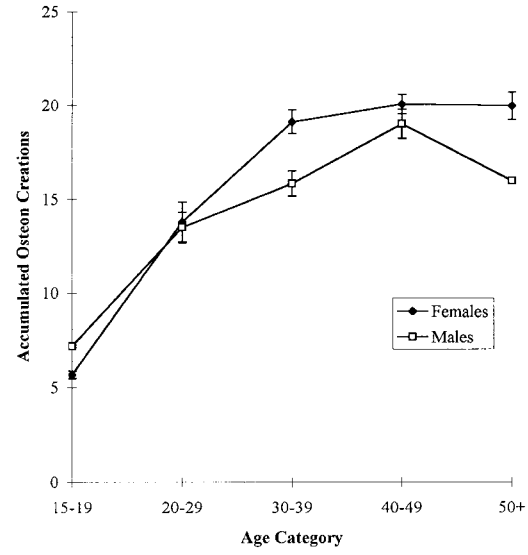

Figure 2. Accumulated osteon creations (n/mm^2) by age and sex.

0.0001), $V_{f,r,t}$ ($P < 0.0001$), and net $V_{f,r,t}$ ($P < 0.01$, females only). Numbers of intact osteons (IO), FR, FO, OPD, AOC, and net $V_{f,r,t}$ all increase with age, whereas μ_{RC} and $V_{f,r,t}$ decrease with age. The number of resorption spaces decreases and then increases with age.

As shown in Figure 1, osteon population density (OPD) differs significantly by age ($P < 0.0001$), increasing over time in both sexes from the second to the sixth decade. This variable reflects the increases in both intact osteons and osteon fragments with age. In females, OPD increases from 5.63/mm^2 to 18.33/mm^2. Male OPD increases from 7.15/mm^2 to 15.53/mm^2.

Accumulated osteon creations (AOC) are significantly different by age in both sexes ($P < 0.001$; Fig. 2). In females, AOC increase from 5.67/mm^2 in the youngest age group to 20.03/mm^2 in the fifth decade, and then decreases slightly to 19.93/mm^2 in the last age group. Male AOC increase from 7.19/mm^2 in the youngest age group to 19.92/mm^2 in the fifth decade, and then decrease to 15.53/mm^2 in the last age group (the last age group is represented by only one individual).

As illustrated in Figure 3, activation frequency (μ_{RC}) differs significantly with age

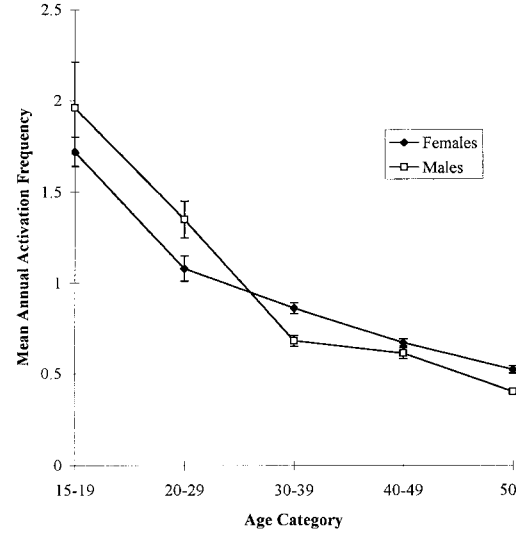

Figure 3. Mean annual activation frequency (n/mm^2/year) by age and sex.

($P < 0.0001$) and decreases over time. In females, μ_{RC} decreases from 1.72/mm^2/year to 0.52/mm^2/year. In males, μ_{RC} decreases from 1.96/mm^2/year to 0.40/mm^2/year.

Figure 4 depicts changes in mean annual bone formation rate ($V_{f,r,t}$). Bone formation rate decreases in both sexes and differs significantly with age ($P < 0.0001$). In females,

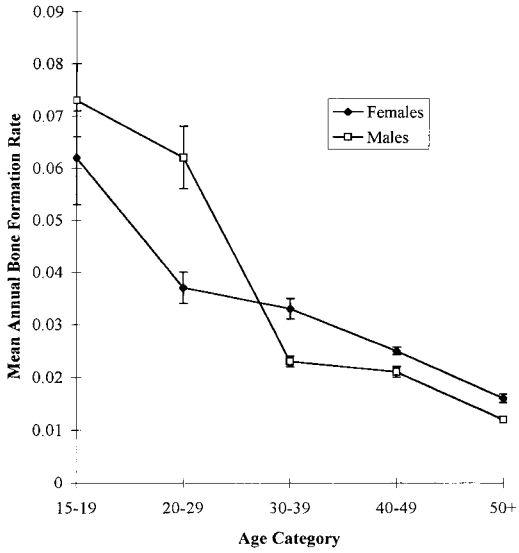

Figure 4. Mean annual bone formation rate (mm^2/mm^2/year) by age and sex.

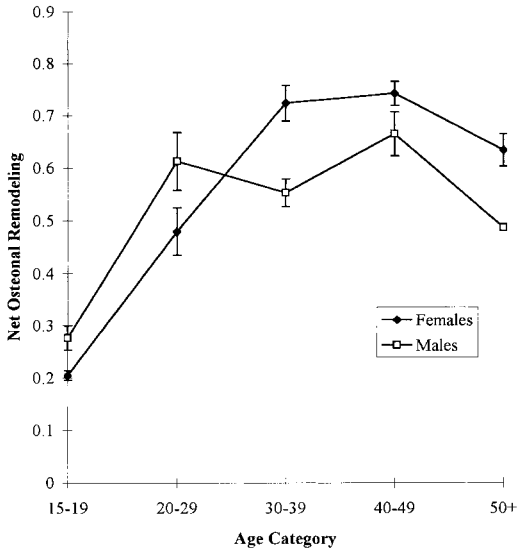

Figure 5. Net osteonal remodeling (mm^2/mm^2) by age and sex.

$V_{f,r,t}$ decreases from 0.062 mm^2/mm^2/year to 0.016 mm^2/mm^2/year. Male $V_{f,r,t}$ decreases from 0.073 mm^2/mm^2/year to 0.012 mm^2/mm^2/year.

Figure 5 shows changes in net osteonal remodeling (net $V_{f,r,t}$) with age. Only females exhibit statistically significant differences with age ($P < 0.01$). Females show an increase in net $V_{f,r,t}$ from 0.204 mm^2/mm^2 to 0.742 mm^2/mm^2 from the second through fifth decades, and then a slight decrease to 0.634 mm^2/mm^2 in the sixth decade.

Sex differences

Table 4 shows the means and standard deviations for all variables for females, males, and combined sexes. The only significant difference between the sexes is in the number of resorption spaces ($P < 0.01$); this is largely due to a dramatic discrepancy during the second decade, with females exhibiting 0.94/mm^2 and males exhibiting 2.31/mm^2 (Fig. 6).

DISCUSSION

Rib bone remodeling at Kulubnarti

The number of intact and fragmentary osteons as well as osteon population density (OPD) and accumulated osteon creations (AOC) increase with age in the rib. Intact osteon number, OPD, and AOC all increase most dramatically between the second and third decade. This pattern has been well-established in the literature (Frost and Wu, 1967; Wu et al., 1970; Stout and Teitelbaum, 1976; Stout and Lueck, 1995) and provides support for the validity of the Kulubnarti sample.

Decreases in mean annual activation frequency and mean annual bone formation rate with age were also observed in the Kulubnarti sample. Again, a number of researchers have reported similar results for both modern and archaeological samples (Frost and Wu, 1967; Wu et al., 1970; Stout and Teitelbaum, 1976; Stout and Lueck, 1995). Bone growth activation and formation occur more frequently in individuals who are still growing (represented by the youngest age category at Kulubnarti). During adulthood, activation frequency probably increases only as a result of mechanical or metabolic necessity (Martin and Burr, 1989). Net osteonal remodeling increases with age, as expected, but decreases slightly in the last decade. This decrease could be due to increased endosteal resorption occurring during the sixth decade.

The number of forming osteons increases with age, and the number of resorption

TABLE 4. Descriptive statistics for females, males and combined sexes[1]

Variables	Female (n = 45)	Male (n = 35)	Combined (n = 80)
IO (n/mm^2)	11.17 ± 0.10	10.68 ± 0.10	10.96 ± 0.05
FR (n/mm^2)	3.35 ± 0.05	3.37 ± 0.07	3.36 ± 0.03
FO (n/mm^2)	1.08 ± 0.02	1.06 ± 0.02	1.07 ± 0.01
RS (n/mm^2)	0.62 ± 0.01	0.73 ± 0.02	0.67 ± 0.007
HcA (mm^2)	0.0011 ± 0.00003	0.0011 ± 0.00005	0.0011 ± 0.00002
OA (mm^2)	0.035 ± 0.0001	0.036 ± 0.0003	0.036 ± 0.0001
A_h (mm^2)	0.034 ± 0.0001	0.035 ± 0.0003	0.035 ± 0.0001
D_h (mm^2)	0.207 ± 0.0006	0.209 ± 0.0008	0.208 ± 0.0003
OPD (n/mm^2)	14.52 ± 0.14	13.88 ± 0.15	14.24 ± 0.07
AOC (n/mm^2)	16.42 ± 0.19	15.86 ± 0.25	16.17 ± 0.10
μ_{RC} (n/mm^2/year)	0.93 ± 0.02	0.89 ± 0.02	0.91 ± 0.009
$V_{f,r,t}$ (mm^2/mm^2/year)	0.034 ± 0.0006	0.034 ± 0.0008	0.034 ± 0.0003
net $V_{f,r,t}$ (mm^2/mm^2)	0.590 ± 0.008	0.578 ± 0.013	0.585 ± 0.005

[1] Values are the mean ± SE. IO, intact osteon number; FR, fragmentary osteon number; FO, forming osteon number; RS, resorption space number; HcA, Haversian canal area; OA, osteon area; A_h, mean osteonal cross-sectional area; D_h, mean osteonal cross-sectional diameter; OPD, osteon population density; AOC, accumulated osteon creations; μ_{RC}, mean annual activation rate; $V_{f,r,t}$, mean annual bone formation rate; net $V_{f,r,t}$, net osteonal remodeling.

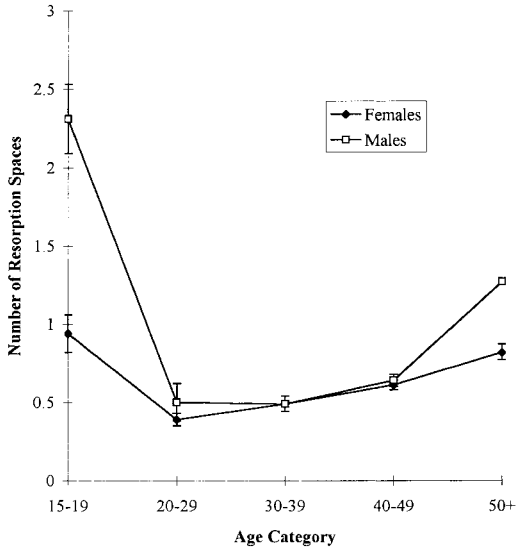

Figure 6. Number of resorption spaces (n/mm^2) by age and sex.

spaces decreases after the second decade and then increases with age. These results, in combination with the observed increase in intact osteon number with age, indicate that older individuals have more porous and more poorly mineralized bone than younger individuals. Higher numbers of canals and resorption spaces contribute to higher porosity, while higher numbers of forming osteons mean that more of the bone is not completely mineralized. These results are expected for several reasons. First, aging-related decreases in hormones such as estrogen and testosterone can derepress bone resorption (Parfitt, 1990). Second, a decrease in the number of osteoblasts present in individuals over 40 and an increase in reversal time contribute to slower osteon formation (Martin and Burr, 1989).

The high number of resorption spaces observed for the youngest age category at Kulubnarti may be a remnant of skeletal development. When combined with other observations for this age category, including a high activation frequency, high bone formation rate, and low number of forming osteons, these results indicate that although resorption is substantial, spaces are quickly replaced by well-mineralized osteons. This pattern is apparent in both sexes, but the number of resorption spaces is higher in males, possibly indicating that males are turning over a higher percentage of bone than females. One explanation for these results is that males are lagging behind girls in skeletal development. This makes sense in light of a study by Van Gerven et al. (1990) that revealed more severe skeletal growth retardation in subadult males compared to females at Kulubnarti.

Comparisons of rib and femur remodeling at Kulubnarti

Morphometric values for the femur are reported in detail by Mulhern and Van Gerven (1997). For consistency, the youngest age category used for the rib was not included in the following comparisons between bones. Osteon population density and net osteonal remodeling are lower in the

femur compared to the rib. Osteon size was not statistically significantly different between bones. Osteon population density in the femur is 11.78 ± 1.80/mm^2 compared to 15.42 ± 1.84/mm^2 in the rib ($P < 0.001$). Net osteonal remodeling in the femur is 0.441 ± 0.067 mm^2/mm^2 in the femur compared to 0.636 ± 0.076 mm^2/mm^2 in the rib ($P < 0.05$).

Pfeiffer (1998) identified significantly larger osteons in the femora than in the ribs of eighteenth- and nineteenth-century skeletons from Spitalfields, London, England, and the St. Thomas Anglican Church, Belleville, Ontario. Different osteon sizes would affect net osteonal remodeling. This pattern was not observed in the Kulubnarti sample between bones, indicating that the observed difference in net remodeling is not due to differences in osteon size.

Lower osteon number and net remodeling in the femur could be due to differences in the effective age of the adult compacta for the two bones. If the femur takes a longer time to mature than the rib, fewer secondary osteons would have accumulated at any given chronological age. Although the effective age of adult compacta is presently unknown for the femur, there is support for an older effective age. Frost (1987a) suggests that the development of a bone is influenced by baseline growth in addition to mechanical usage. The more extreme mechanical demands of the femur, therefore, may lengthen the period of cortical drift and rapid bone modeling.

Significant differences between the sexes observed in osteon number and size for the femur by Mulhern and Van Gerven (1997) were not observed for the rib. In the femur, males have significantly more intact osteons (9.74/mm^2) compared to females (6.73/mm^2; $P < 0.0001$). Also, femoral mean osteonal cross-sectional area is significantly larger in females (0.038 mm^2) compared to males (0.034 mm^2; $P < 0.05$).

The presence of these kinds of sexual morphometric differences in the femur has also been reported by Burr et al. (1990) in a Pecos Indian sample. In the Pecos study, higher intact osteon numbers in males and larger osteons in females were both identified as adjustments that enhance structural support of the femur in this physically active population. The Kulubnarti population was also intensely physically active, and the similarities between the two may reflect microstructural adaptations to mechanical demands.

Populational comparisons of rib remodeling

Stout and Lueck (1995) reported bone remodeling data for three archaeological populations, including the Ledders, Gibson, and Windover sites, and one modern sample. These sites represent a variety of geographic locations, time periods, and subsistence patterns. The Ledders and Gibson sites, located in the Lower Illinois River Valley, date to the Late Woodland (A.D. 1000) and Middle Woodland (50 B.C.–A.D. 400) periods, respectively. The Windover site, in East-Central Florida, dates from 6900–8120 B.P. The Ledders population practiced maize agriculture, and the groups from Gibson and Windover were intensive foragers. The Kulubnarti population falls roughly between the Gibson and Ledders populations temporally (550–1450 A.D.), and it is most similar to Ledders in subsistence pattern, although millet, wheat, and barley (instead of maize) are the staple crops.

Stout and Lueck (1995) suggest that the lower OPD and AOC observed in archaeological samples may indicate that skeletal maturity was reached at a later age in ancient times than it is today. If this is the case, the authors argue, then annual mean activation rates and bone formation rates would appear to be low if the constant 12.5, which was established based on modern samples, is used as the effective age of the birth of adult compacta.

The Kulubnarti results are consistent with the values for archaeological samples reported by Stout and Lueck (1995). Mean annual bone formation rate in the Kulubnarti sample is 0.034 mm^2/mm^2/year, a value consistent with those reported for the Gibson and Windover archaeological samples, which are 0.038 and 0.039 mm^2/mm^2/year, respectively. The Kulubnarti bone formation rate is somewhat lower than the rate for the Ledders population of 0.065 mm^2/

mm^2/year, and much lower than the modern sample, with a bone formation rate of 0.102 mm^2/mm^2/year. The Kulubnarti sample exhibits a smaller mean osteonal cross-sectional area (0.035 mm^2) than the modern sample (0.040 mm^2), but a slightly larger area than the Ledders sample (0.033 mm^2), so osteon size cannot explain the observed differences in bone formation rates.

A number of factors may contribute to the differences observed between the Kulubnarti and other archaeological populations, including differences in the effective age of the adult compacta, genetic differences, differences in childhood bone mass development, differences in the minimum effective strain (MES) setpoint required to repress bone remodeling, and differences in the frequency of strains exceeding the MES.

First, the effective age of the adult compacta could have been older in ancient times. Frost (1987a) suggests that a bone's development is influenced by both growth and mechanical usage. On an individual level, an older effective age could result from a longer period of modeling during growth, increasing bone gain during childhood and representing a developmental adaptation to a physically demanding lifestyle. This is consistent with the mechanostat theory of Frost (1987c), which maintains that bone modeling increases under repeated high strains. On a populational level, underlying genetic factors could also potentially regulate the effective age of adult compacta.

A second contributing factor could stem from genetically based populational differences in bone formation rates. Populational differences in bone formation rates have been reported, even among modern populations. Weinstein and Bell (1988) report differences in a modern sample of blacks and whites in bone formation activity. Specifically, they observed that bone formation rates in blacks were 35% of that in whites, which resulted in higher bone density in the former.

Parfitt et al. (1997) provide an alternative explanation for the apparent bone-remodeling differences between ethnic groups, which provides a third candidate for explaining the observed differences. These researchers suggest that the apparent differences in bone-cell function observed between blacks and whites are the result of genetic differences in bone formation during growth. Specifically, the development of higher bone mass during growth would result in less fatigue microdamage, resulting in less need for repair and lower bone turnover rates.

A fourth possibility is that the Kulubnarti population has a lower minimum effective strain (MES) setpoint compared to other populations. Frost (1987c) discusses the possibility that genetic factors may be responsible for low MES setpoints, which would explain the higher bone mass in some populations. A low MES setpoint would mean that lower strains could increase bone modeling and depress remodeling, resulting in denser bone.

Finally, the frequency of strains exceeding the MES setpoint must be considered as a potentially contributing factor to populational differences in bone formation rates. According to the mechanostat theory (Frost, 1987c), activation of bone remodeling decreases and bone formation is repressed under repeated strains above the MES setpoint. The Kulubnarti geographical context and skeletal remains both provide support for a highly physically active population. Traversing extremely rugged terrain and maneuvering steep riverbanks, 20–25 m high (Adams, 1994), was a part of everyday life at Kulubnarti. High frequencies of degenerative joint disease (Kilgore, 1984) and fractures (Burrell et al., 1986; Kilgore et al., 1997) characterize the skeletal remains.

A combination of influences is necessary to explain the remodeling dynamics at Kulubnarti when compared to other populations. The Kulubnarti population undoubtedly experienced mechanical strain, but it was probably not significantly more severe than the strain experienced by the Gibson, Windover, and Ledders populations. The presence of populational genetic differences that influence bone development, maturation, and maintenance provide a plausible explanation for the observed differences in bone remodeling.

CONCLUSIONS

Rib-remodeling dynamics were studied for an archaeological sample from Kulubnarti, Nubia, of medieval antiquity. Overall patterns of bone remodeling with respect to age were consistent with previous studies documenting increases in osteon numbers and resorption spaces over time, as well as decreases in mean annual activation and bone formation rates. A high number of resorption spaces in young males compared to females may reflect differences in skeletal development, with boys lagging behind girls.

Comparisons of rib and femur morphometrics show that the femur has fewer osteons and lower net remodeling. This difference could simply reflect a difference in age of maturation of the two bones, with the rib reaching maturity earlier than the femur. The more intensive functional demands of the femur could prolong the period of modeling and drift relative to the rib.

In the femur, females have fewer, but larger, intact osteons. This kind of morphometric sexual dimorphism was not observed in the rib. Similar results were also reported in a Pecos Indian population by Burr et al. (1990). It is not possible to identify the factors responsible for these differences, although it appears that both males and females are well-adapted to a physically active lifestyle.

Populational comparisons indicate that the Kulubnarti population experienced low bone activation and formation rates, with values consistent with those reported for two archaeological samples studied by Stout and Lueck (1995). It is possible that a combination of factors, including a higher effective age of the adult compacta, low minimum effective strain (MES) setpoint, and repeated strains above the MES setpoint, may have contributed to the low remodeling rates at Kulubnarti, potentially reflecting adaptations to a highly physically active lifestyle.

ACKNOWLEDGMENTS

The author thanks Dennis Van Gerven, David Greene, Bert Covert, and Darna Dufour for their advice and comments on earlier drafts of this work. Thanks are also extended to Jim Harrington for preparation of thin sections as well as Richard Jones and James Hanken for making available the necessary image-analyzing equipment. Preparation of thin sections was partially funded by a grant from the Graduate School at the University of Colorado at Boulder.

LITERATURE CITED

Abbott S, Trinkaus E, Burr DB. 1996. Dynamic bone remodeling in later Pleistocene fossil hominids. Am J Phys Anthropol 99:585–601.

Adams WY. 1977. Nubia: corridor to Africa. Princeton: Princeton University Press. 797 p.

Adams WY. 1994. Kulubnarti I: the architectural remains. Lexington, KY: Program for Cultural Resource Assessment, University of Kentucky. 342 p.

Burr DB, Ruff CB, Thompson DD. 1990. Patterns of skeletal histologic change through time: comparison of an archaic Native American population with modern populations. Anat Rec 226:307–313.

Burrell LL, Mass MC, Van Gerven DP. 1986. Patterns of long bone fracture in two Nubian cemeteries. Hum Evol 1:495–506.

Frost HM. 1987a. Secondary osteon populations: an algorithm for determining mean bone tissue age. Yrbk Phys Anthropol 30:221–238.

Frost HM. 1987b. Secondary osteon population densities: an algorithm for estimating missing osteons. Yrbk Phys Anthropol 30:239–254.

Frost HM. 1987c. Bone "mass" and the "mechanostat": a proposal. Anat Rec 219:1–9.

Frost HM, Wu K. 1967. Histological measurements of bone formation rates in contemporary archaeological and paleontological compact bone. In: Woode WD, editor. Miscellaneous papers in paleopathology. Flagstaff: Museum of Northern Arizona. p 9–22.

Galai. 1991. Cue-2 Olympus Image Analyzer Software.

Kilgore L. 1984. Degenerative joint disease in a medieval Nubian population. Ph.D. dissertation. University of Colorado, Boulder, CO.

Kilgore L, Jurmain R, Van Gerven DP. 1997. Palaeoepidemiological patterns of trauma in a medieval Nubian skeletal population. Int J Osteoarchaeol 7:103–114.

Martin DL. 1983. Paleophysiological aspects of bone remodeling in the Meroitic, X-Group and Christian populations from Sudanese Nubia. Ph.D. dissertation. University of Massachusetts, Amherst, MA.

Martin DL, Armelagos GJ. 1979. Morphometrics of compact bone: an example from Sudanese Nubia. Am J Phys Anthropol 51:571–578.

Martin RB, Burr DB. 1989. Structure, function and adaptation of compact bone. New York: Raven Press. 275 p.

Mulhern DM. 1994. The effects of environment and culture on patterns of microscopic histologic change in human bone: a comparison of a late Christian Nubian population with archaeological and modern populations. M.A. thesis. University of Colorado, Boulder, CO.

Mulhern DM, Van Gerven DP. 1997. Patterns of femoral bone remodeling dynamics in a medieval Nubian population. Am J Phys Anthropol 104:133–146.

Parfitt AM. 1990. Bone-forming cells in clinical conditions. In: Hall BK, editor. Bone volume I: the osteoblast and osteocyte. Caldwell, NJ: Telford Press. p 193–302.

Parfitt AM, Han ZH, Palnitkar S, Rao DS, Shih MS, Nelson D. 1997. Effects of ethnicity and age or menopause on osteoblast function, bone mineralization, and osteoid accumulation in iliac bone. J Bone Miner Res 12:1864–1873.

Pfeiffer S. 1998. Variability in osteon size in recent human populations. Am J Phys Anthropol 106:219–227.

Prendergast-Moore K. 1987. Osteopenia in a medieval population from Kulubnarti, Sudan. Ph.D. dissertation. University of Colorado, Boulder, CO.

Stout SD. 1976. Histomorphometric analysis of archaeological bone. Ph.D. dissertation. Washington University, St. Louis, MO.

Stout SD. 1978. Histological structure and its preservation in ancient bone. Curr Anthropol 19:600–604.

Stout SD, Lueck R. 1995. Bone remodeling rates and skeletal maturation in three archaeological skeletal populations. Am J Phys Anthropol 98:600–604.

Stout SD, Paine RR. 1994. Brief communication: bone remodeling rates: a test of an algorithm for estimating missing osteons. Am J Phys Anthropol 93:123–129.

Stout SD, Teitelbaum SL. 1976. Histomorphometric determination of formation rates of archaeological bone. Calcif Tissue Res 21:163–169.

Van Gerven DP, Sanford MK, Hummert JR. 1981. Mortality and culture change in Nubia's *Batn el Hajar*. J Hum Evol 10:395–408.

Van Gerven DP, Hummert JR, Prendergast-Moore K, Sanford MK. 1990. Nutrition, disease, and the human life cycle: a bioethnography of a medieval Nubian community. In: DeRousseau J, editor. Primate life history and evolution. New York: Wiley-Liss. p 297–323.

Weinstein RS, Bell NH. 1988. Diminished rates of bone formation in normal black adults. N Engl J Med 319: 1698–1701.

Wu K, Schubeck KE, Frost HM, Villaneuva A. 1970. Haversian bone formation rates determined by a new method in a mastodon and in human diabetes mellitus and osteoporosis. Calcif Tissue Res 6:204–219.